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Analysis of the dental morphology of Plio-Pleistocene hominids

II. Mandibular molars – study of cusp areas, fissure pattern and cross sectional shape of the crown

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INTRODUCTION

The aim of this series of papers is twofold: first, to establish and document, by means of a detailed and precise morphometric survey of the available, well preserved, material, the distinctive dental characteristics of early hominid taxa; secondly, to use the characteristics of these reference populations as a guide for assessing the affinities of specimens whose taxonomic designation is controversial.

The first paper in this series (Wood & Abbott, 1983) recorded the results of conventional and planimetric measurements of the overall size and shape of mandibular molar crowns, and also examined the incidence and expression of morphological traits. In the present paper, the investigation is carried a stage further with a detailed study of the relative size of individual cusps, and analyses of both the pattern of the primary fissure system and the shape of the molar crowns seen in coronal cross section.

MATERIALS AND METHODS

Fossil sample

This analysis was based on a sample of 196 mandibular molar crowns (71 $M_{\overline{1}}$s; 60 $M_{\overline{2}}$s; 65 $M_{\overline{3}}$s). Specimens were either allocated to one of six informal taxonomic categories, or classed as 'unknown'. Details of provenance, criteria for inclusion and taxonomic allocations are given in the first paper (Wood & Abbott, 1983).

The more detailed measurements used in this analysis could, however, be made only on smaller subsets of the published taxonomic categories, and on fewer of the specimens in the 'unknown' group. An inventory of specimens from each of the four major categories which are included in this study is given below:

(1) $M_{\overline{1}}$: EAFROB – KNM-ER 802, 3230, 3890; Peninj: SAFROB – TM 1517; SK 6 (R) and (L), 23 (R) and (L), 25 (R) and (L), 34 (R) and (L), 55 (R) and (L), 61, 63 (R) and (L), 104, 828, 838, 843, 846, 3974. SAFGRA – Sts 9, 24, 52, Stw 1; MLD 2 (R) and (L). EAFHOM – KNM-ER 806, 820 (R) and (L), 992 (R) and (L), 1502, 1507; OH 7 (R) and (L), 13, 16. $M_{\overline{2}}$: EAFROB – KNM-ER 729, 1171, 1816, 3230; Peninj (R) and (L). SAFROB – TM 1600; SK 1, 5, 6 (R) and (L), 23 (R) and (L), 25, 34 (R) and (L), 37, 55, 843, 858, 1586 (R) and (L), 3976. SAFGRA – Sts 4, 52 (R) and (L); MLD 2 (R) and (L), 24. EAFHOM – KNM-ER 806, 992 (R) and (L); OH 7, 13, 16. $M_{\overline{3}}$: EAFROB – KNM-ER 729 (R) and (L), 802, 810, 1509,

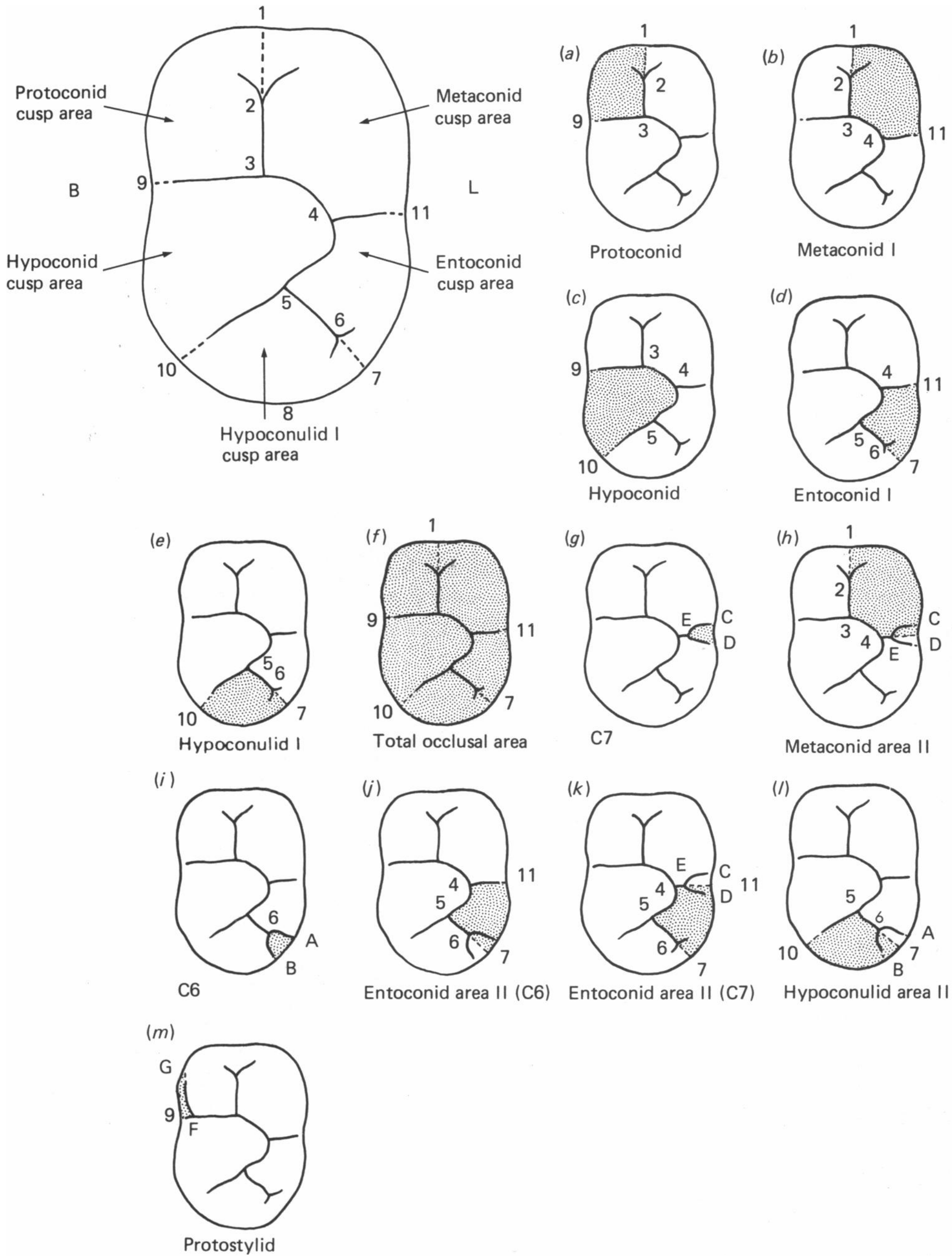

Fig. 1. Diagrams illustrating the measured areas of the main and additional cusps of mandibular molar teeth. All diagrams refer to a left tooth.

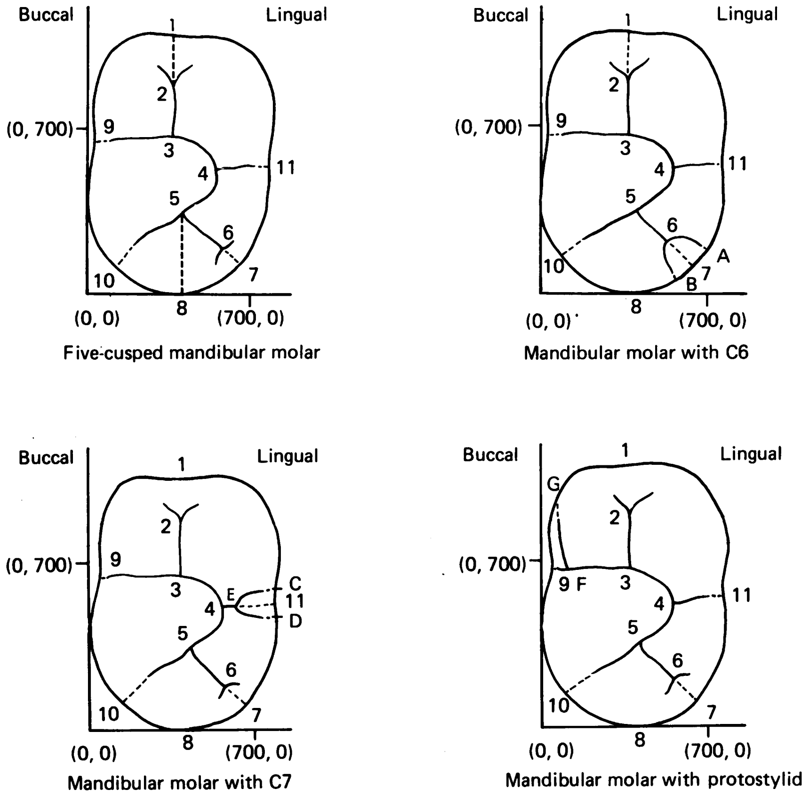

Fig. 2. Diagrams illustrating the reference points used to define the pattern of the major fissures.

3230; Peninj (R) and (L). SAFROB – TM 1517; SK 6 (R) and (L), 12, 23 (R) and (L), 34 (R) and (L), 75, 840, 841, 843, 844, 880, 1586. SAFGRA – Sts 14, 55, 1518, 1520, Stw 3, 14; MLD 18, 19. EAFHOM – KNM-ER 730, 806 (R) and (L), 992 (R) and (L); OH 4, 13 (R) and (L), 16 (R) and (L).

In some of the analyses, in particular the multivariate studies, the specimens were entered as individual cases. This was done with the intention of trying to identify and define morphological patterns and assess affinities without making *a priori* taxonomic judgements. However, if, as in many cases, no discrete clusters resulted from such analyses, then the results were interpreted with reference to the taxonomic attributions set out in the previous paper.

Cusp areas

The surface area of the individual cusps was measured from specially prepared occlusal photographs, and was used as an estimate of cusp size (details of the technique used to prepare the enlarged prints are given in the first paper (Wood & Abbott, 1983)). The boundaries of each cusp were marked on the photographs by tracing the course of the primary fissures and by locating the reference points which are illustrated in Figures 1 and 2, and defined in Table 1. These particular reference points have been chosen for their general applicability to hominoid molars. Some are the same as those defined by Biggerstaff (1969), but others were specifically devised

Table 1. *Definitions of the reference points located on the crown margin and on the fissures separating the main cusps*

1. The point on the mesial border of the crown opposite the centre of the mesial fovea.
2. The centre of the mesial fovea, or the junction of the mesial longitudinal fissure and the mesiolingual and mesiobuccal foveal fissures.
3. The intersection of the mesial longitudinal fissure with the mesiobuccal fissure.
4. The centre of the central fossa, or the junction of the lingual fissure with the mesiobuccal and distobuccal fissures.
5. The intersection of the distal longitudinal fissure and the distobuccal fissure.
6. The posterior fovea, or the intersection of the distal longitudinal fissure with the buccal and lingual foveal fissure, or, in teeth with C6, the intersection of the distal longitudinal fissure with the fissure delimiting the C6.
7. The point on the border of the crown which is closest to the posterior fovea (i.e. point 6).
8. The point on the distal border of the crown which is directly distal to the intersection of the distal longitudinal fissure and the distobuccal fissure (i.e. point 5).
9. The point on the buccal border of the crown located opposite the termination of the mesiobuccal occlusal fissure.
10. The point on the distobuccal border of the crown at the termination of the distobuccal occlusal fissure.
11. The point on the lingual border of the crown which is located opposite the termination of the lingual occlusal fissure. When a C7 is present the fissures delimiting it are ignored, and the reference point is located opposite the point where the main lingual fissure bifurcates around the C7.

Table 2. *Definitions of the reference points located on the crown margin and on the fissures delineating accessory cusps and the protostylid*

(A) The point on the distolingual border of the crown located opposite the termination of the mesial C6 fissure.
(B) The point on the distal border of the crown located opposite the termination of the most distal C6 fissure.
(C) The point on the lingual border of the crown located opposite the termination of the mesial C7 fissure.
(D) The point on the lingual border of the crown located opposite the termination of the distal C7 fissure.
(E) The point of intersection of the C7 fissure with the main lingual fissure.
(F) The intersection of the protostylid groove with the mesiobuccal fissure.
(G) The point on the mesiobuccal border of the crown which marks the intersection of the protostylid groove with the mesiobuccal border, or which would mark this intersection when the line of the fissure demarcating the protostylid is projected to the crown border.

for this study. In those teeth with a C6, C7 or protostylid, additional landmarks were defined on the occlusal photographs; these are also illustrated in Figures 1 and 2 and defined in Table 2. In teeth which showed significant interproximal wear, the outlines of the original mesial and/or distal crown borders were reconstructed by reference to both the overall shape of the preserved crown and the extent and orientation of the interproximal wear facet(s).

When accessory cusps were present two sets of measurements were made. In the first set, the areas of the accessory cusps and the main cusps were measured separately (Fig. 1 *a–e*; *g*; *i*; *m*). In the second set, the area of any accessory cusp was divided between the two adjacent main cusps (Fig. 1 *h*; *j*; *k*; *l*). This was done by projecting the line of the primary fissure separating the main cusps to the margin of the crown. This deliberate 'simplification' of the area of a tooth was carried out in order to allow comparison between the maximum number of fossil specimens.

Cusp areas were measured on the photographic prints, using a fixed-arm planimeter. The average of three readings was taken for each measurement, and then reduced to original size by dividing by the square of the enlargement factor for each occlusal photograph. Tests showed that measurement error represented approximately 1 % of the total variance. The individual cusp areas, the sum of the individual cusp areas and the total occlusal area (on some teeth it was possible to measure the area of the whole tooth despite the fact that damage or wear had obliterated the fissures defining one or more cusps) were then recorded on computer cards.

For each molar, simple descriptive statistics of the absolute cusp areas were computed for the whole sample and the taxonomic categories to check for measurement and transcription errors. However, our interest lay not so much in the absolute size of the cusps (for the sum of these is simply the overall size of the crown), but in any differences in relative cusp size. The data were, therefore, mainly analysed in terms of relative cusp size, the area of each cusp being expressed as a percentage of the total occlusal area. The mean, standard deviation, standard error and range of the relative cusp areas were calculated for each of the four major taxonomic categories, and the significance of any differences between categories was assessed using Student's *t* test. The absolute and relative cusp areas of teeth in the taxonomic categories and in the 'unknown' group were then analysed separately by computing the principal components of the covariance matrix (PCm) and by studying the pattern of Pythagorean distances between specimens.

Fissure pattern

The patterns of the primary fissures were compared by analysing the X/Y co-ordinates of defined points on the fissure system and crown margin. In view of the variations in the incidence of accessory cusps, this analysis did not include information about the secondary fissures associated with these cusps. Tracings of the fissure system and the crown outline were made from the occlusal photographs, and the positions of points 1–11 were clearly marked on the tracings (Figs. 1 and 2; Tables 1 and 2). To simplify the data analysis, the differences between left and right teeth were eliminated by mirror-imaging teeth from the right side. A coordinate reference frame and an origin for each tracing were defined in the following way. Each tooth tracing was orientated with its mesiodistal axis perpendicular to the X axis, and positioned so that the most distal point on the crown was touching the X axis. The Y axis was then positioned so that it passed through the most buccal point on the crown. The intersection of the axes served as the origin (0, 0) for the co-ordinate analysis, and, for purposes of calibration, marks were made on both axes 7 cm from the origin (Fig. 2).

The tracings were analysed on a PCD-Type 1B digitizer. In order to compensate for minor differences in magnification of the occlusal photographs, the digitizer was calibrated using the 7 cm marks. The X/Y co-ordinates of each reference point were then recorded and transferred to computer cards. All tracings were made by the same observer, but interpretations of the fissure pattern were always checked with a second person. Checks on the measurement technique have established that errors in the co-ordinate plotting are minimal.

The co-ordinates used to define the fissure pattern and crown outline were analysed by 'Procrustes' analysis (Gower, 1975). This technique undertakes a pairwise comparison of the patterns of reference points. They are enlarged, translated and rotated so that the sum of the squared distances between homologous points is minimized. The algorithm defines the centroid (or 'centre of gravity') of each pattern as the mean of the X and Y co-ordinates of all the points. Differences in size are

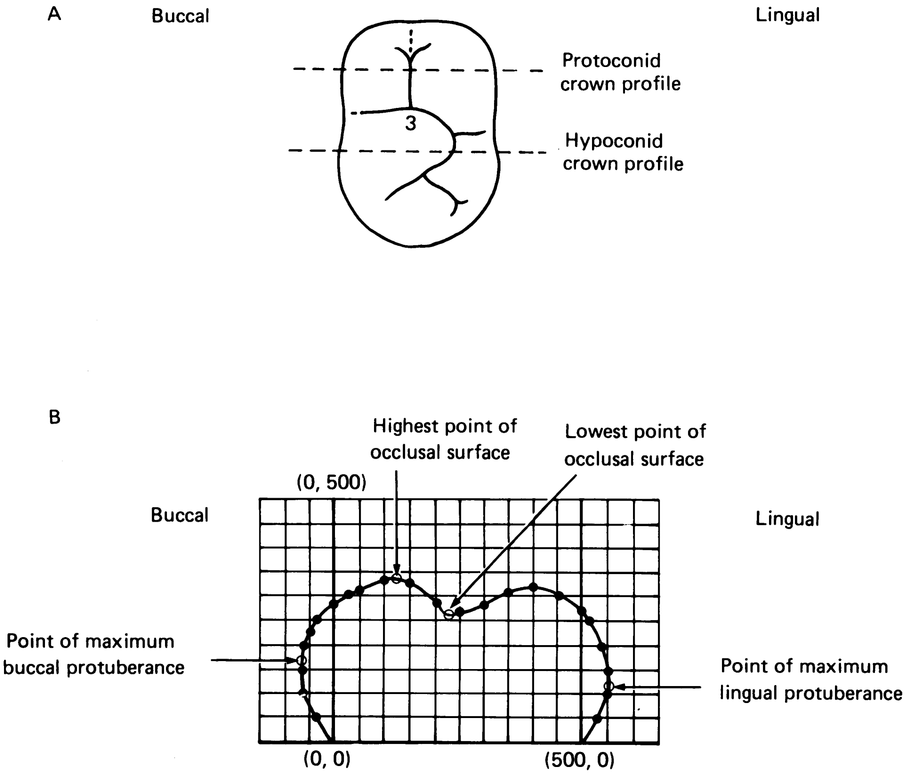

Fig. 3. Diagram to show (A) the planes of sectioning, and (B) the protocol, for recording points on the crown profile of mandibular molars.

eliminated by expanding or contracting the image ('enlargement') so that the sum of the squared distances between each point and the centroid is equal to unity. The centroids of each pair are then lined up ('translation'), and finally the pattern of points is rotated around the axis of the centroid ('rotation') until the sum of the squared distances between the landmarks is minimized. In this case, because all the points are in two dimensions, finding the 'rotation' is simply a matter of finding a single angle. 'Procrustes' analysis can also 'reflect' the image, but this was unnecessary in this study because the tracings of the right teeth have been mirror-imaged at an earlier stage of an analysis.

The sum of the squared distances is an expression of 'likeness' between each pair of tooth crowns, and these pairwise comparisons are combined to form a similarity matrix. In this study, the complex relationships between teeth expressed in the matrix have been portrayed in two ways. In the first, the tooth crowns were represented by points which were plotted using axes which preserve the maximum amount of information about relationships (so called principal coordinates, PCd, (Gower, 1966)). In the second method, each tooth was matched with the six teeth most similar to it. A subroutine then arranged these in rank order, and displayed the results in the form of a nearest neighbours table.

Shape of crown profile

Suggestions in the literature that the height of the crown and the shape of its buccal and lingual surfaces may differ between early hominid taxa have never been

Table 3. *Relative cusp areas of hominid mandibular molars by taxonomic group*

	Protoconid					Metaconid II					Hypoconid					Entoconid II					Hypoconulid II				
	X	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.	*X*	*N*	S.D.	Min.	Max.
$M_{\bar{1}}$																									
EAFROB	20·9	4	2·4	18·2	24·0	22·0	4	1·3	20·8	23·4	19·7	4	1·7	18·4	22·3	19·3	3	2·7	16·9	22·2	18·8	4	3·3	15·3	22·5
SAFROB	21·2	20	1·5	19·2	24·4	22·2	20	1·3	19·3	24·5	21·4	20	1·5	18·7	24·2	17·1	20	1·8	13·8	20·2	18·0	20	1·4	15·5	21·4
SAFGRA	23·5	5	0·9	22·6	24·9	24·3	5	1·2	23·1	25·9	21·6	6	1·3	19·8	23·7	15·6	6	3·8	11·3	20·5	15·4	6	2·7	12·2	18·4
EAFHOM	24·4	11	2·0	20·5	28·2	23·8	11	1·8	21·4	27·4	22·7	11	1·6	19·8	25·1	15·3	11	1·7	13·3	18·2	14·5	11	2·0	10·9	17·1
$M_{\bar{2}}$																									
EAFROB	22·0	5	1·4	20·4	23·7	23·3	5	1·8	21·0	25·8	18·8	5	0·6	18·1	19·5	20·4	6	3·1	15·7	24·3	14·6	5	2·6	11·2	17·9
SAFROB	23·4	16	1·8	19·9	26·3	22·1	16	1·7	19·1	25·0	20·3	16	1·0	18·9	22·0	17·3	16	2·4	12·1	20·8	16·7	16	2·1	13·4	20·2
SAFGRA	25·3	6	2·5	22·7	29·1	22·9	6	1·9	20·3	24·7	21·2	6	1·4	19·2	22·7	16·0	6	1·4	13·7	17·4	14·5	6	1·7	12·0	16·7
EAFHOM	25·8	6	1·5	23·6	27·3	22·8	6	2·1	20·9	26·1	20·4	6	0·9	19·3	21·7	15·9	6	2·0	13·4	19·0	15·3	6	2·1	12·7	17·6
$M_{\bar{3}}$																									
EAFROB	21·3	8	3·5	16·2	27·3	22·6	8	1·9	19·7	25·6	14·9	8	1·3	12·8	17·0	21·7	7	1·9	19·1	25·0	20·4	7	3·1	15·5	25·0
SAFROB	23·0	15	2·0	20·4	26·7	23·5	14	2·5	18·6	28·7	18·6	14	3·5	14·6	27·5	15·6	12	3·8	11·1	22·9	18·5	12	2·9	13·7	22·8
SAFGRA	24·0	6	1·8	22·0	27·3	22·9	5	3·6	18·3	26·8	18·7	7	1·6	16·5	20·8	18·3	4	4·3	13·2	23·3	15·2	6	3·2	11·5	19·1
EAFHOM	25·6	10	3·1	21·2	30·9	23·9	9	2·0	20·0	26·4	17·2	10	1·0	16·0	18·8	15·7	9	3·5	10·1	20·7	18·0	9	2·0	15·2	22·5

The sample sizes do not always accord with the numbers of specimens listed in the Materials and Methods section. The damaged teeth which have been excluded are listed below, with the missing cusps in parentheses:

$M_{\bar{1}}$: EAFROB – KNM-ER 802 (Ent). SAFGRA; Stw1 (Prot and Met).

$M_{\bar{2}}$: EAFROB – Pening L. (Prot, Met, Hyp, Hld). SAFROB; SK 858 (Ent and Hld), SK 3976 (Prot, Met, Hyp).

$M_{\bar{3}}$: EAFROB – KNM-ER 810 (Ent and Hld). SAFROB; SK 12 (Met, Ent and Hld), 34 (Ent and Hld), 1586 (Ent, Hyp and Hld). SAFGRA – MLD 4 (Prot, Met and Ent), 18 (Met and Ent) and 19 (Ent, Hld).

systematically investigated. We therefore examined the profiles of coronal sections taken at two places on the crown. The cervical margin was chosen as the baseline for the profiles, and thus teeth were included in this part of the study only if the cervical line could be identified both buccally and lingually.

All suitable teeth were cast, using dental alginate and dental stone. Check measurements on the casts and the originals showed that the average distortion of molar buccolingual diameters was $+1{\cdot}9\%$ (range $-0{\cdot}5\%$ to $+3{\cdot}2\%$). Two cross sections of each tooth crown were prepared, one across the protoconid/metaconid, and the other at the level of the hypoconid/entoconid. The sites of the sections were located with respect to the mesial and distal borders and reference point 3 on the fissure system (Figs. 1, 2; Table 1) which marks the intersection of the fissure separating the protoconid and metaconid with the fissure dividing the mesial cusps from the hypoconid. Pencil marks were made on the mesiodistal axis of the tooth midway between point 3 and point 1, and one third of the distance between point 3 and point 8. Pencil lines were then drawn over the crown in a buccolingual direction at these two sites (Fig. 3A). The sections were cut with a piercing saw just distal to the mark, and were then sanded down to the pencilled line with fine emery paper. The outlines of the sections were carefully traced onto paper, and the locations of the cervical line on the buccal and lingual surfaces were clearly marked. The profiles were then photographed, and each negative was projected onto squared paper (using a photographic enlarger) so that the buccolingual diameter at the cervical line measured 50 mm. The images of profiles of left molars were mirror-imaged so that in all the final drawings buccal is to the left and lingual to the right (Fig. 3B). Points were marked on the profile where it intersected the vertical or horizontal reference grid; for the sides of the profiles intersections with the horizontal lines were marked, and for the occlusal surface the vertical lines were used to locate the intersections (as shown in Fig. 3B). The highest and lowest points on the occlusal surface and the points of maximum buccal and lingual projection were marked. The X and Y co-ordinates of all these points thus provided a reasonable metrical summary of the shape of the cross sections.

RESULTS

Cusp areas

Univariate analysis

A statistical summary of the relative size of the main cusps for each of the four major taxonomic categories is given in Table 3. The significance of the differences in mean values have been examined using pairwise t tests, and the results of these are presented in Table 4. Inspection of the mean values shows that there is a trend in the results for the two 'robust' categories (whose mandibular molar teeth are larger overall) to have relatively smaller mesial cusps, but a relatively large entoconid and hypoconulid. The trend is most marked in the $M_{\bar{1}}$s (Fig. 4), and least in the $M_{\bar{3}}$s. This interpretation is confirmed by the results of the t tests. Between-group comparisons of relative cusp areas show that for all three tooth types there are a number of significant differences between taxonomic categories. Although the increase in relative size of the distal main cusps in the two 'robust' categories is clearly influenced by the contribution of accessory distal cusps in these taxa, when the areas of the entoconid and hypoconulid are considered without the areas of the adjacent accessory cusps a modest, but statistically insignificant, increase in relative cusp size still remains.

Table 4. *Between group comparisons of relative cusp areas: significance values based on 't' tests using pooled variances and two-tailed model*

	Protoconid				Metaconid II				Hypoconid				Entoconid II				Hypoconulid II			
	EAFR	SAFR	SAFG	EAFH	EAFR	SAFR	SAFG	EAFH	EAFR	SAFR	SAFG	EAFH	EAFR	SAFR	SAFG	EAFH	EAFR	SAFR	SAFG	EAFH
$M_{\bar{1}}$																				
EAFROB	—				—				—				—				—			
SAFROB	N.S.	—			N.S.	—			N.S.	—			N.S.	—			N.S.	—		
SAFGRA	0·05	< 0·01	—		< 0·05	< 0·01	—		N.S.	N.S.	—		N.S.	N.S.	—		N.S.	< 0·01	—	
EAFHOM	< 0·05	< 0·001	N.S.	—	N.S.	< 0·01	N.S.	—	< 0·01	< 0·05	N.S.	—	< 0·01	< 0·01	N.S.	—	N.S.	< 0·001	N.S.	—
$M_{\bar{2}}$																				
EAFROB	—				—				—				—				—			
SAFROB	N.S.	—			N.S.	—			< 0·01	—			< 0·05	—			N.S.	—		
SAFGRA	< 0·05	N.S.	—		N.S.	N.S.	—		< 0·01	N.S.	—		< 0·01	N.S.	—		N.S.	< 0·05	—	
EAFHOM	< 0·01	< 0·01	N.S.	—	N.S.	N.S.	N.S.	—	< 0·01	N.S.	N.S.	—	0·01	N.S.	N.S.	—	N.S.	N.S.	N.S.	—
$M_{\bar{3}}$																				
EAFROB	—				—				—				—				—			
SAFROB	N.S.	—			N.S.	—			0·01	—			0·001	—			N.S.	—	—	
SAFGRA	N.S.	N.S.	—		N.S.	N.S.	—		< 0·001	N.S.	—		N.S.	N.S.	—		0·01	< 0·05	—	
EAFHOM	0·01	< 0·05	N.S.	—	N.S.	N.S.	N.S.	—	0·001	N.S.	< 0·05	—	0·001	N.S.	N.S.	—	N.S.	N.S.	N.S.	—

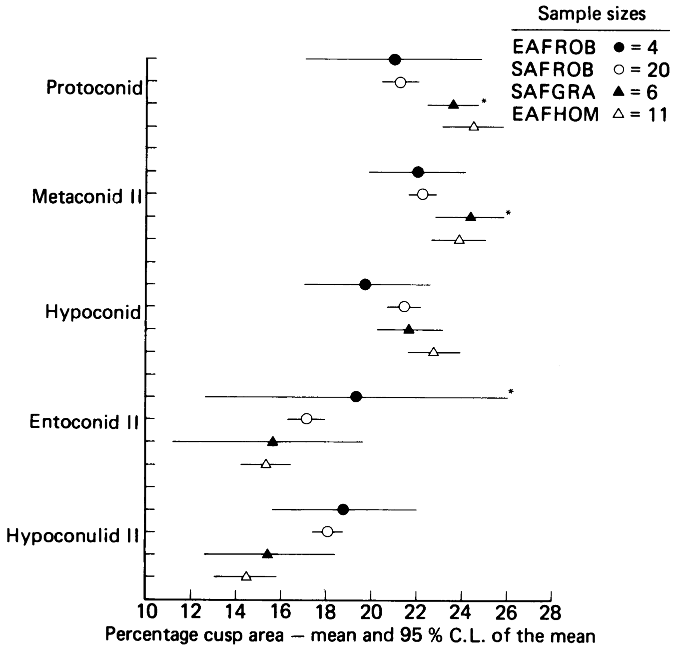

Fig. 4. The mean value and 95 % confidence interval of the relative area of the main cusps for each of the major hominid taxonomic categories. The sample sizes of the taxa marked with an asterisk are one smaller than the numbers given at the head of the Figure.

The relative sizes of the accessory cusps and protostylid in the four major taxonomic categories are given in Table 5. In the $M_{\bar{1}}$s the two samples of 'robust' australopithecines are the only taxonomic categories in which a C6 is present, and the results suggest that these cusps make up a similar percentage of the total occlusal area in the two taxa. The C6s of the 'robust' $M_{\bar{2}}$s are similar in relative size to those of the $M_{\bar{1}}$s. The few C6s which occur among the $M_{\bar{2}}$s of SAFGRA and EAFHOM tend to be relatively smaller than those of the 'robust' taxa, but the samples are small and the differences are not statistically significant. For $M_{\bar{1}}$ there is no significant correlation between the size of a C6 and total occlusal area, either within any of the taxonomic groups, or when the whole sample is considered together. However, for the pooled samples of $M_{\bar{2}}$s and $M_{\bar{3}}$s a significant correlation ($P = < 0{\cdot}001$) was found within each tooth type, but in neither case did within-group correlation coefficients reach statistical significance. The larger C6 values in the $M_{\bar{3}}$s of the two 'robust' categories are due, in some of the specimens, to there being more than one accessory distal cusp, whereas, in others, there is a single larger C6.

The relative size of the C7 shows little variation between taxonomic categories, and is around 5 % of the total occlusal area in all three types of molar; there are no significant correlations with overall tooth size. The distribution of the relative surface area of the protostylid confirms the results of the earlier study (Wood & Abbott, 1983) which suggested that although a protostylid was more common in SAFROB than SAFGRA, when it does occur in the 'gracile' australopithecines it is better developed. The pooled sample of $M_{\bar{2}}$s is the only one in which the area of the protostylid is significantly correlated ($P < 0{\cdot}05$) with total occlusal area.

Table 5. *Relative size of accessory cusp and protostylid, expressed as a percentage of the total occlusal area, for the four major taxonomic categories of Plio-Pleistocene hominids*

	C6					C7					Prostostylid				
	$\bar{X}$	N	S.D.	Min.	Max.	$\bar{X}$	N	S.D.	Min.	Max.	$\bar{X}$	N	S.D.	Min.	Max.
EAFROB															
$M_{\bar{1}}$	6·4	3	2·5	3·6	8·1	—	—	—	—	—	1·8	1	—	—	—
$M_{\bar{2}}$	5·9	6	2·7	3·0	10·8	—	—	—	—	—	1·3	1	—	—	—
$M_{\bar{3}}$	11·7	7	4·2	6·6	16·9	—	—	—	—	—	—	—	—	—	—
SAFROB															
$M_{\bar{1}}$	5·8	11	2·5	3·1	10·9	5·5	2	0·9	4·8	6·2	3·4	7	1·2	2·1	4·8
$M_{\bar{2}}$	6·5	11	2·1	2·6	10·8	—	—	—	—	—	3·4	9	1·5	1·1	2·7
$M_{\bar{3}}$	10·5	3	3·9	6·0	13·1	6·4	1	—	—	—	3·3	5	1·3	1·8	4·7
SAFGRA															
$M_{\bar{1}}$	—	—	—	—	—	—	—	—	—	—	6·4	2	1·4	5·4	7·4
$M_{\bar{2}}$	4·9	3	1·0	3·9	5·9	4·3	2	0·6	3·9	4·7	5·8	2	0·5	5·4	6·1
$M_{\bar{3}}$	6·9	4	0·9	6·0	8·2	5·1	4	3·4	3·3	10·1	—	—	—	—	—
EAFHOM															
$M_{\bar{1}}$	—	—	—	—	—	5·4	3	0·3	5·3	5·8	3·5	1	—	—	—
$M_{\bar{2}}$	4·7	2	1·3	3·7	5·6	4·2	3	1·3	2·8	5·2	6·8	1	—	—	—
$M_{\bar{3}}$	8·1	5	2·9	5·1	12·1	4·2	2	0·7	3·7	4·6	5·0	2	0·7	4·5	5·5

Table 6. *Percentage contribution to total variance and eigen-vector scores of the first and second principal components derived from the abolute and relative cusp area data*

	Absolute cusp area						Relative cusp area					
	PCmI			PCmII			PCmI			PCmII		
	$M_{\bar{1}}$	$M_{\bar{2}}$	$M_{\bar{3}}$	$M_{\bar{1}}$	$M_{\bar{2}}$	$M_{\bar{3}}$	$M_{\bar{1}}$	$M_{\bar{2}}$	$M_{\bar{3}}$	$M_{\bar{1}}$	$M_{\bar{2}}$	$M_{\bar{3}}$
Eigen-values												
Percentage variance	74	85	79	14	7	8	59	56	49	23	28	24
Eigen-Vectors												
Protoconid	−0·33	−0·41	−0·38	0·54	−0·56	0·42	−0·56	0·59	−0·4	−0·03	−0·25	0·28
Metaconid II	−0·43	−0·47	−0·47	0·22	−0·26	0·49	−0 24	0·20	−0·25	−0·03	−0·32	−0·16
Hypoconid	−0·44	−0·39	−0·25	0·40	−0·27	0·39	−0·26	0·16	−0·31	0·37	0·25	−0·56
Entoconid II	−0·43	−0·57	−0·59	−0·64	0·73	−0·59	0·50	−0·74	0·81	−0·65	−0·44	−0·27
Hypoconulid II	−0·58	−0·35	−0·47	−0·30	0·12	−0·29	0·56	−0·21	0·16	0·60	0·76	0·71

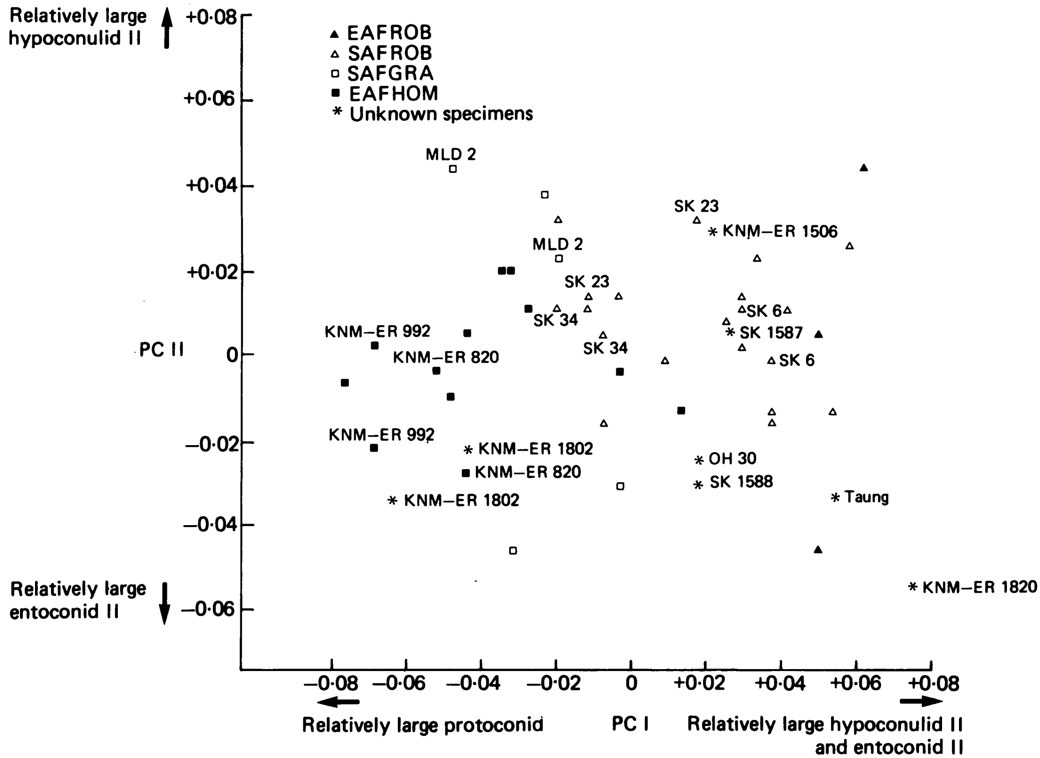

Fig. 5. Plot of the first (PCm I) and second (PCm II) principal components generated from the relative cusp area data of hominid mandibular first molars.

Multivariate analysis

In the Principal Components Analysis of the actual cusp areas for each of the three molar types the first principal component (PCmI) accounted for approximately 80 % of the total variance (Table 6). The elements of the components are all equal in sign, and approximately equal weight is given to each of the cusps. This suggests, therefore, that the major separating effect is size (Jolicoeur & Mosimann, 1960; Gould, 1975; Wood, 1978). For all three molar types, the plots of PCmI and PCmII show a spread of the teeth along PCmI such that teeth from the two larger-toothed 'robust' taxa tend to lie towards one pole, while the smaller teeth from the other taxa lie towards the other. When the PCmI scores for individual teeth are compared with the total occlusal area for each tooth, it is clear that the two values are linked and their rank orders are similar. In contrast, the arrangement of specimens along PCmII (which accounts for around 10 % of the variance) and PCmIII are such that there is complete intermixing of the taxa.

For relative cusp area, the resulting PCmIs account for a smaller percentage of the total variance than for the absolute cusp area data. The elements of the eigenvectors for both PCmI and PCmII are also different in that they are mixed in both size and sign, suggesting that both these principal components contain information about tooth shape. Inspection of the plots for each molar type reveals a scattered distribution in which there are no obvious clusters, and so the plots have been interpreted using the established taxonomic groupings. The separation of the

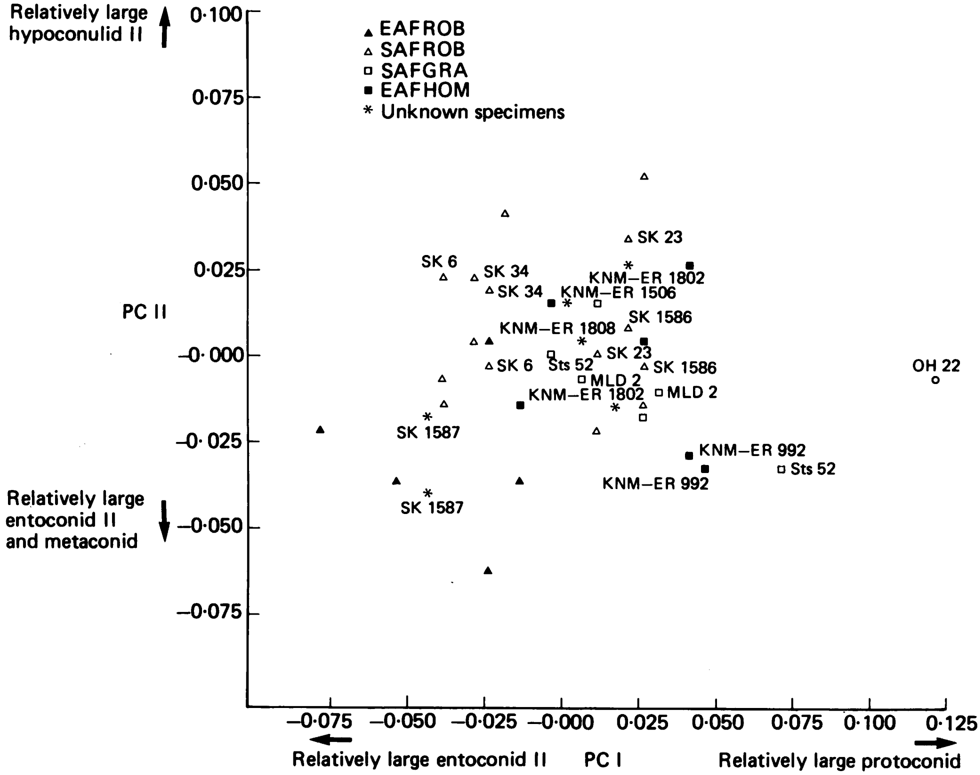

Fig. 6. Plot of the first (PCm I) and second (PCm II) principal components generated from the relative cusp area data of hominid mandibular second molars.

taxonomic categories is greatest for $M_{\bar{1}}$, with the $M_{\bar{2}}$s and $M_{\bar{3}}$s showing progressively more overlap (Figs. 5, 6). When PCmI and PCmII are plotted for the $M_{\bar{1}}$s (Fig. 5), the major taxonomic categories are distributed from the negative to the positive end of PCmI in order EAFHOM, SAFGRA, SAFROB, and EAFROB. The component loadings (Table 6) indicate that teeth with a relatively large protoconid cluster at the negative pole, whereas teeth with positive scores on PCmI have relatively large hypoconulids and entoconids; these findings thus concur with those of the univariate analysis (Fig. 3). The distribution of specimens and taxonomic categories within the total hyperspace can be judged from the matrix of Pythagorean distances. The distance between group means and the average distance between specimens in each taxonomic category (with and without antimeres) are given in Table 7. The distribution of specimens which have both the right and left teeth preserved is also of interest, and such specimens are identified by their museum number in the PCm plots (Figs. 5, 6).

The matrix of intercusp correlations for the pooled sample of $M_{\bar{1}}$s can be represented diagrammatically (Fig. 7) and underlines the contrast in behaviour between the distal cusps (Hld and Ent) and the remaining cusps. The pattern of the correlations is such that the mesial cusps have strong negative correlations with the hypoconulid and entoconid, thus contrasting with the positive correlations within the mesial and distal groups of cusps.

Table 7. *Table of Pythagorean distances derived from the covariance matrix for* $M_{\bar{1}}$*s and* $M_{\bar{2}}$*s*

		Distances between group centroids				Average distance between members of a taxonomic category			
						All teeth		Excluding antimeres	
		EAFROB	SAFROB	EAFHOM	SAFGRA	$\bar{X}$	S.D.	$\bar{X}$	S.D.
$M_{\bar{1}}$	EAFROB	—				0·066	0·022	0·091	0·0
	SAFROB	0·036	—			0·045	0·015	0·048	0·016
	EAFHOM	0·089	0·054	—		0·054	0·019	0·059	0·016
	SAFGRA	0·078	0·044	0·025	—	0·061	0·026	0·067	0·027
$M_{\bar{2}}$	EAFROB	—				0·056	0·017	0·049	0·018
	SAFROB	0·053	—			0·055	0·02	0·062	0·024
	EAFHOM	0·069	0·032	—	—	0·053	0·017	0·045	0·013
	SAFGRA	0·068	0·037	0·013		0·056	0·016	0·046	0·0

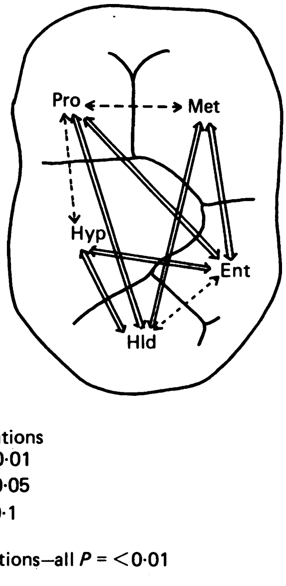

Fig. 7. Pattern of intercusp correlations for hominid mandibular first molars.

Fissure pattern

Plots based on the pairwise measure of similarity for $M_{\bar{1}}$ and $M_{\bar{2}}$ are shown in Figures 8 and 9. Once again no discrete groupings result, but the sample does distribute in a way which can be readily interpreted in terms of the taxonomic categories. Although the percentage variance accounted for by the PCdIs (37 % in $M_{\bar{1}}$ and 29 % in $M_{\bar{2}}$) is rather low, it is still useful for sorting taxa. Strongly positive scores on the first axis are associated with teeth which have a relatively distally positioned posterior fovea and a mesial longitudinal fissure which lies towards the lingual border. These differences in fissure pattern are thus directly related to a general increase in the relative contribution of the mesial cusps and are best illustrated by comparing teeth

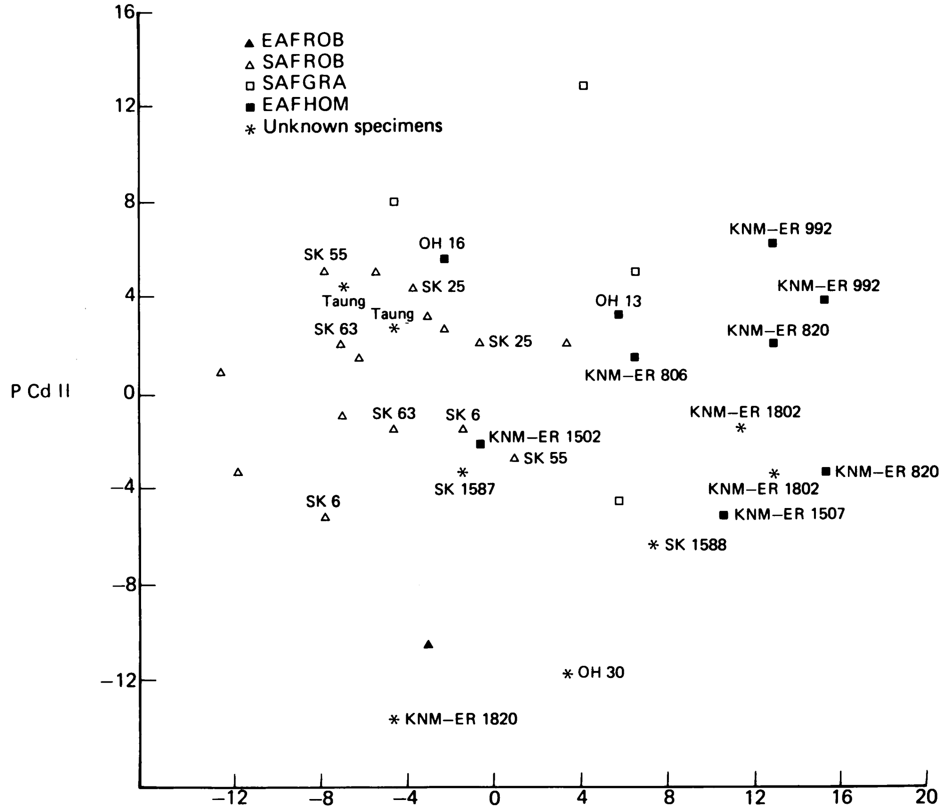

Fig. 8. Principal coordinate plot of hominid $M_{\bar{1}}$ fissure pattern data.

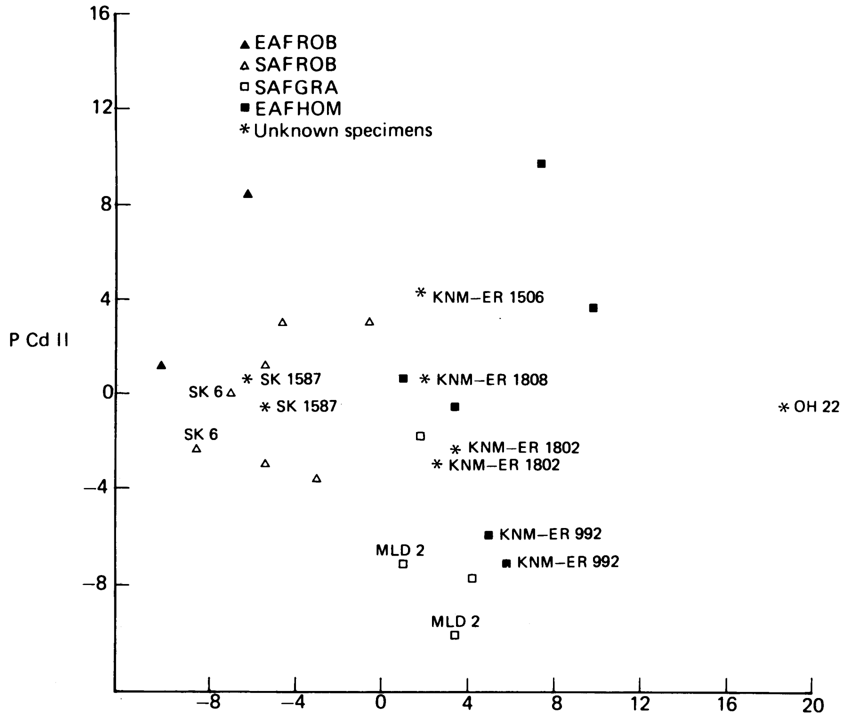

Fig. 9. Principal coordinate plot of hominid $M_{\bar{2}}$ fissure pattern data.

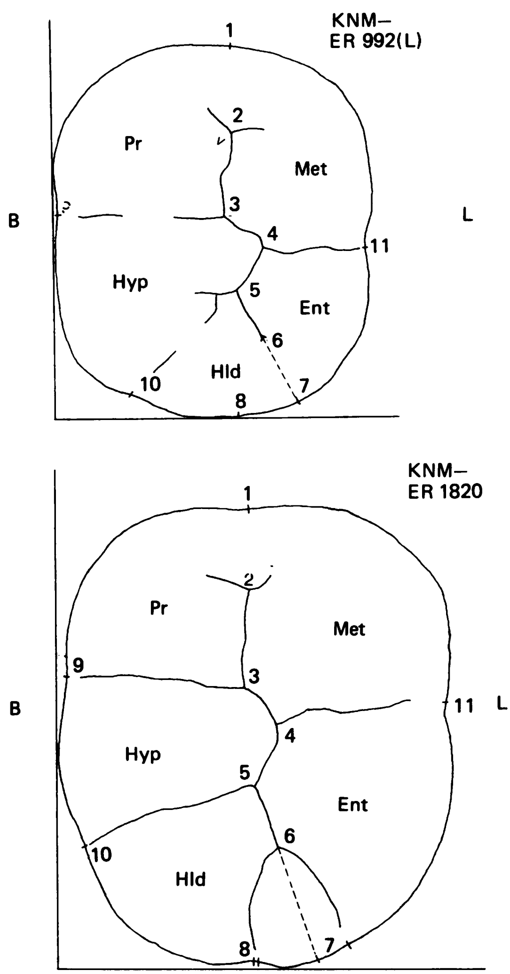

Fig. 10. Specimens illustrating the range of variation of the fissure pattern of hominid mandibular first molars.

which are widely separated in the two plots (Figs. 10, 11). Thus, the evidence from the shape of the fissure pattern reflects in another way the basic changes in relative cusp area referred to in the previous section. The results of both these plots and the list of nearest neighbours suggest that, for the majority of specimens in which both right and left teeth are preserved, a tooth lies relatively close to its antimere in terms of this particular measure of similarity.

Crown profile

The simplest, and perhaps also the most productive, way of analysing the crown profiles is by direct visual comparison. The tooth types with the largest sample sizes are the $M_{\bar{1}}$s and $M_{\bar{3}}$s, and the available protoconid and hypoconid profiles of the four main taxonomic categories have been drawn to unit width in Figures 12, 13. In the case of the $M_{\bar{1}}$s, reliable observations can be made only on the two taxa with the larger sample sizes, SAFROB and EAFHOM. Nonetheless, both taxa are remarkably consistent in the shape of the buccal and lingual crown borders. At the

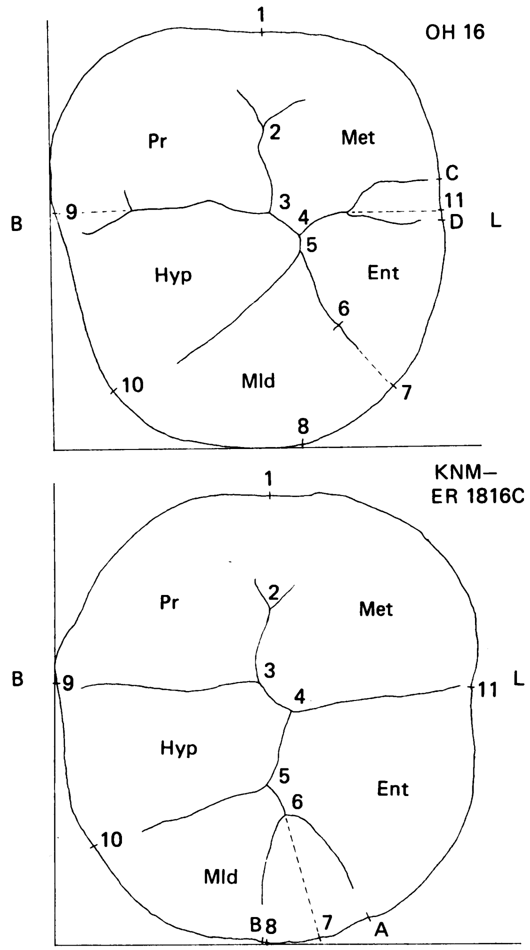

Fig. 11. Specimens illustrating the range of variation of the fissure pattern of hominid mandibular second molars.

level of both the protoconid and the hypoconid, the crown profiles of the SAFROB category are symmetrical so that the buccal border first rises nearly vertically and reaches its maximum convexity only some 10 mm above the plane of the cervical line. In the sections of the EAFHOM $M_{\bar{1}}$s taken at the level of the protoconid, however, the point of greatest convexity of the buccal border is closer to the cervical line, with the result that the point of greatest buccal projection is near to the base of the tooth.

The pattern of the $M_{\bar{3}}$ coronal profiles within the SAFROB group is, with a single exception for both the protoconid and the hypoconid, also remarkably consistent. The shape of the buccal border at the level of both the protoconid and hypoconid does, however, differ from that of the $M_{\bar{1}}$s. In the $M_{\bar{3}}$s, the widest part of the crown is at, or just above, the cervical margin, and, from that point, the buccal surface inclines gradually upwards and inwards. The shape of the crown profiles of the EAFHOM group shows much greater variation for $M_{\bar{3}}$ than for $M_{\bar{1}}$, and no consistent pattern can be discerned. The larger EAFROB $M_{\bar{3}}$ sample has protoconid

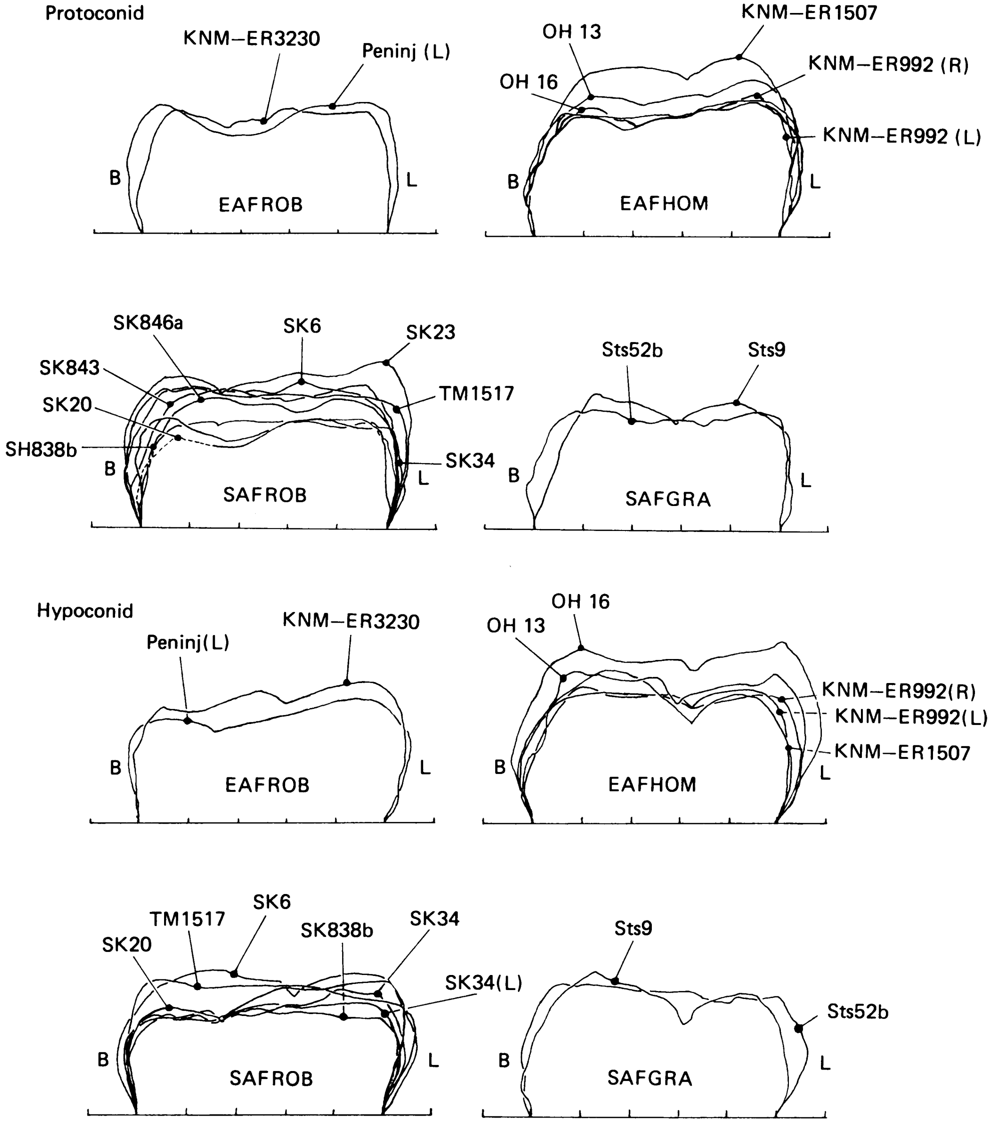

Fig. 12. Profiles of cross sections through the crowns of hominid first mandibular molars arranged according to taxonomic group.

and hypoconid coronal profiles which are similar to those noted for the SAFROB $M_{\overline{1}}$s, with relatively steep-sided and evenly curved buccal and lingual borders. The more vertical buccal border at the level of the protoconid in EAFROB is thus in marked contrast to the more sloping border of the $M_{\overline{3}}$s of the SAFROB group.

DISCUSSION

While the length, breadth and computed area of a tooth crown are the most commonly used metrical devices for describing an individual tooth, or the dental characteristics of a proposed hominid taxon, these relatively crude estimates of size

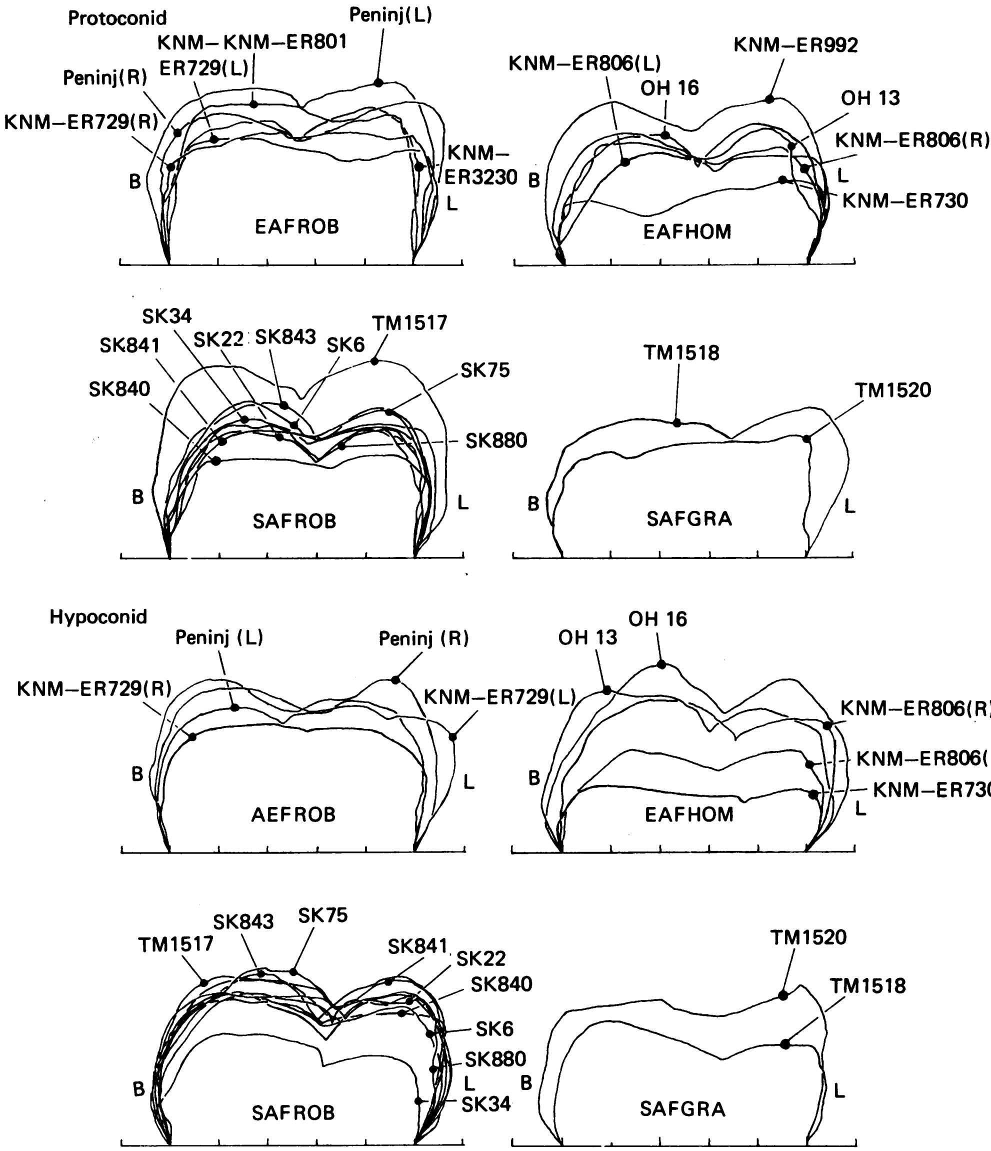

Fig. 13. Profiles of cross sections through the crowns of hominid third mandibular molars arranged according to taxonomic group.

by no means exhaust the morphological information which tooth crowns can provide. This is not to say that size can never be useful taxonomically and indeed there are indications from an earlier part of this investigation (Wood & Abbott, 1983) that overall size may be adequate to distinguish the taxonomic categories EAFROB and EAFHOM. Nonetheless, in the same paper it was also apparent that the presence, number and type of additional cusps bore no simple relationship to overall tooth size, and offered the prospect of contributing to the definition of early hominid taxa and thus the diagnosis of individual specimens. While we are aware that relative cusp size, fissure pattern and crown profile shape may be highly correlated with cusp number and the location of additional cusps, we consider that the precision, relative objectivity and size-independence of the measurements described in the present study make them particularly suitable for exploring patterns of morphological variation within early hominid dental remains.

Sperber (1974) and Corruccini & McHenry (McHenry & Corruccini, 1980*a*, *b*; Corruccini & McHenry, 1980) have also attempted to define tooth shape, but they based their attempts on either cusp diameters or a series of diagonal and width measurements of the molar crown. Such measurements, however, inevitably lack the precision and accuracy of techniques which make measurements of cusp area and use co-ordinate analysis to define the position of reference points. Nonetheless, they provide a most useful check on the results obtained in this study.

In the first paper in this series we outlined, and defended, our reasons for adopting the strategy of sacrificing sample size in order to make more detailed observations and measurements. Clearly, the problem is exacerbated in the present study when teeth could be included only if the combination of wear and preservation allowed the identification of individual cusps and fissures. Nonetheless we are still convinced that the reasons for our decision are no less valid and consider that our results, together with those of studies using simple measurements made on more specimens, both have a useful role to play in the analysis of hominid remains.

Relative cusp size

Inspection of the relative cusp areas of each of the four major taxa shows that the $M_{\bar{1}}$s and $M_{\bar{2}}$s of the two 'robust' australopithecine taxa combine a relative reduction of the trigonid (i.e. a small protoconid and metaconid II) with an increase in the area of the talonid (i.e. a large hypoconulid II and entoconid II). This trend is still apparent even when the area of additional cusps is not included in that of the adjacent principal cusps. It is, however, evident from the high incidence of the tuberculum sextum in these molars, that the increasing size of the talonid is either due to, or results in, the additional infolding of the enamel organ epithelium which results in a tuberculum sextum.

The differences in relative size of the trigonid and talonid in the 'robust' taxa, which have on average larger molar tooth crowns than SAFGRA and EAFHOM, suggest that this change may be an allometric, or size-related, phenomenon. To investigate this, we have studied the relationship between relative cusp size and overall tooth size in modern *Homo sapiens*, *Gorilla* and *Pongo* but the results suggest that there is no such clear allometric trend in these comparative samples. This does not rule out allometric size relationships as the reason for the differences in relative cusp size in the fossil hominid taxa, but the evidence from the comparative groups does indicate that such an association is unlikely. Thus, we suggest the alternative working hypothesis that this particular pattern or relative cusp size in the mandibular molar crowns may be part of a broader functional, and presumably diet-related, adaptation in the 'robust' australopithecines.

Two observations about the relative size of the tuberculum sextum can be added to the conflicting evidence for the relationship between overall tooth size and the number and size of additional cusps which has already been cited in the earlier paper. First, in neither of the two 'robust' taxa is there any consistent relationship along the molar tooth row between the relative size of additional distal cusps and the overall size of the tooth crowns. Secondly, there are no significant differences in the relative size of a C6 between $M_{\bar{1}}$s and $M_{\bar{2}}$s of the two 'robust' taxa even though in overall size the $M_{\bar{2}}$s are respectively 21 % and 13 % larger than the $M_{\bar{1}}$s. Conversely, although in both 'robust' taxa the relative size of the C6 is greater in the $M_{\bar{3}}$s than in the $M_{\bar{2}}$s, these two types of teeth differ hardly, if at all, in overall size.

The additional lingual cusp, the C7, is consistent in its relative size (about 5 %) in the three taxa in which it occurs, and does not appear to increase in relative size in the $M_{\bar{3}}$s (*contra* the behaviour of the C6 in the 'robust' taxa). In the tooth types in which C6s and C7s occur together, they occupy similar proportions of the total crown area. The area of the protostylid is, however, more variable, tending to be relatively smaller in EAFROB, and larger in SAFGRA and EAFHOM.

When Sperber (1974) examined plots of the mean cusp diameters he concluded that they revealed no consistent pattern that would serve to identify groups. The conclusions of McHenry & Corruccini (1980*a*, *b*) and Corruccini & McHenry (1980), however, are in agreement with the results of the present study in finding that both *Australopithecus robustus* and *Australopithecus boisei* show a decrease in the relative size of the trigonid (protoconid and metaconid) and an increase in the size of the talonid (hypoconulid). There is, however, less agreement between the results of the studies when other cusps are considered. Whereas the results presented here suggest that entoconid II is larger, and the relative size of the hypoconid smaller, in the 'robust' teeth, McHenry & Corruccini's interpretation of their canonical variate loadings suggests the reverse relationship, i.e. a larger hypoconid and a smaller entoconid in the 'robust' australopithecines. Different methods of measuring the size of main and additional cusps may, however, underlie the discrepancies between the two sets of results.

The results of the Principal Components Analysis of the relative areas of the major cusps (with the areas of additional cusps allocated to adjacent main cusps) are shown in Figures 5 and 6. For the $M_{\bar{1}}$s the main axis of taxonomic separation of the major taxonomic categories is parallel to the PCmI, whereas for the $M_{\bar{2}}$s PCmI and PCmII both contribute to the separation. The plot of the $M_{\bar{3}}$s shows almost complete intermixing of taxonomic categories.

McHenry & Corruccini (1980*a*) and Corruccini & McHenry (1980) also used multivariate methods to analyse their data, but they used the shape component of the Penrose statistic as a measure of distance, and Canonical Variates Analysis of shape variables (that is a *Q*-mode procedure standardized after removing allometric residuals by regression (Corruccini, 1978*b*)) to derive a series of independent orthogonal axes. They also included in these analyses data other than those taken from molar crowns (e.g. $P_{\bar{3}}$, and mandibular dimensions). Despite these differences in both technique and data however, their results (Corruccini & McHenry, 1980, Fig. 4, p. 216) agree with ours and show a similar distribution of taxa, with *Australopithecus boisei* at one end of the taxonomic cline and *Homo habilis* at the other.

Fissure pattern

The plots using the first two axes for $M_{\bar{1}}$ and $M_{\bar{2}}$ (Figs. 8, 9) of the fissure pattern data show a similar distribution of taxa to that seen in the principal component plots of the relative cusp area (except that the $M_{\bar{1}}$ PCd plot is a mirror-image). The plots in Figures 8 and 9 can be interpreted by referring back to the fissure patterns of the specimens clustered at either end of axis I. Inspection of the patterns shows that the relative position along the mesiodistal axis of the mesiobuccal and distobuccal fissures and the posterior fovea, and the situation of the mesial longitudinal fissure either centrally, or towards the lingual border, are among the features which determine the position of teeth in the plots (Figs. 10, 11). The close correspondence between the results of analysing the fissure pattern and the relative cusp area data underlines the strong and obvious correlation between fissure pattern and the presence of additional cusps, and further evidence of this will be presented when 'unknown' specimens are discussed.

Coronal crown profiles

Differences in the shape of the lingual and buccal surface of mandibular molar crowns were noted by Robinson (1956; p. 118) when he related the 'flatter' slope of the buccal surface of the 'gracile' australopithecine crown to the presence of the protoconidal cingulum. Howell (1978) is one of the few subsequent authors to refer to the shape of the sides of the mandibular molar crown, but he merely comments that the $M_{\overline{3}}$s of *Australopithecus robustus* from Swartkrans have "vertical sides".

The size of the $M_{\overline{1}}$ samples in the present study allow useful comparisons to be made between SAFROB and EAFHOM, and, of these two groups, it is the molars of the EAFHOM category which have the reduced curvature on the buccal face. The influence of cingulum development on the shape of the buccal face is not easy to assess, but can be investigated by studying the relationship, if any, between crown shape and the incidence and expression of the protostylid. Reference to Wood & Abbott (1983) shows, however, that a protostylid is recorded in half the $M_{\overline{1}}$s in both the SAFROB and EAFHOM categories. As far as the effect of a protostylid on the shape of the buccal face is concerned, the evidence from the EAFHOM group is not convincing, for though the slope of this surface is similarly convex in all five teeth, none is recorded as having a marked, shelf-like protostylid.

Evidence of the influence of the cingulum on the shape of the buccal surface of the mesial part of the crown in $M_{\overline{3}}$s is equally conflicting. The relatively steep buccal sides of the EAFROB category could be linked with the absence of a shelf-like protostylid in this group, but the more sloping buccal surfaces of the SAFROB category are not associated with any greater development of the protostylid.

Different degrees of wear preclude any detailed comparisons of crown height, but it is noticeable that in the larger $M_{\overline{3}}$ sample of EAFROB, when the teeth are reduced to the same buccolingual breadth, there appears to be little evidence for the conclusion of Howell (1978; p. 176) that the mandibular molar cusps of *Australopithecus boisei* were 'low'. Wallace (1975, 1978) and Robinson (1963) have also referred to taxonomic differences in molar cusp height, and concluded that the cusps of the SAFROB category were lower than those of the South African 'gracile' australopithecines. These conclusions were, however, based simply on inspection of the intact tooth, but there are too few 'gracile' teeth in our own crown profile sample to enable this claim to be verified.

Affinities of 'unknown' specimens

The results of both the previous study by Wood & Abbott (1983) (which concentrated metrically on the overall size of mandibular molar crowns) and the present one (which has emphasized aspects of relative cusp size and crown shape) show clearly that any contrasts between the mandibular molars of early hominid taxa are aspects of an essentially continuous distribution of size and shape differences. However, within the two major geographical areas of eastern and southern Africa the differences between the 'robust' australopithecines and the respective smaller-toothed

Table 8. *Taxonomic affinities of teeth in the 'unknown' category*

Specimen	Type	Crown area	Additional cusps	Relative cusp area	Fissure pattern	Crown profile
Koobi Fora						
KNM-ER 1462	$M_{\overline{3}}$	EAFHOM	EAFROB/EAFHOM (C6)	—	—	—
KNM-ER 1467	$M_{\overline{3}}$	EAFROB	NA	—	—	NA
KNM-ER 1480	$M_{\overline{3}}$	EAFHOM	EAFROB/EAFHOM (C6)	—	—	NA
KNM-ER 1506	$M_{\overline{1}}$	EAFHOM	EAFHOM (C7/no C6)	EAFROB/EAFHOM	NA	EAFHOM
	$M_{\overline{2}}$	EAFHOM	EAFHOM (C7/no C6)	EAFHOM	EAFHOM	—
KNM-ER 1801	$M_{\overline{3}}$	EAFROB	NA	—	—	NA
KNM-ER 1802	$M_{\overline{1}}$ (R)	EAFHOM	EAFHOM (C7/no C6)	EAFHOM	EAFHOM	EAFHOM
	$M_{\overline{1}}$ (L)	EAFHOM	EAFHOM (C7/no C6)	EAFHOM	EAFHOM	EAFHOM
	$M_{\overline{2}}$ (R)	EAFROB/ EAFHOM	EAFROB/EAFHOM (C6 and C7)	EAFHOM	EAFHOM	—
	$M_{\overline{2}}$ (L)	EAFHOM	EAFROB/EAFHOM (C6/no C7)	EAFHOM	EAFHOM	—
KNM-ER 1812	$M_{\overline{3}}$	EAFHOM	EAFROB/EAFHOM (C6/no C7)	—	—	NA
KNM-ER 1820	$M_{\overline{1}}$	EAFROB	EAFROB (C6/no C7)	EAFROB	EAFROB	NA
KNM-ER 2601	$M_{\overline{3}}$	EAFHOM	EAFHOM (C7/no C6)	—	—	NA
Olduvai						
OH 27	$M_{\overline{3}}$	EAFHOM	EAFHOM (C6 and C7)	—	—	NA
OH 30	$M_{\overline{1}}$	EAFROB	EAFROB (C6)	EAFHOM/EAFROB	EAFROB	NA
Swatkrans						
SK 1587	$M_{\overline{1}}$	SAFROB/ SAFGRA	SAFROB (C6/no C7)	SAFROB	SAFROB	SAFROB
	$M_{\overline{2}}$ (R)	SAFROB/ SAFGRA	SAFROB (C6/no C7)	SAFROB	SAFROB	—
	$M_{\overline{2}}$ (L)	SAFROB/ SAFGRA	SAFROB (C6/no C7)	SAFROB	SAFROB	—
SK 1588	$M_{\overline{1}}$	SAFROB/ SAFGRA	SAFROB/SAFGRA (no C6)	SAFROB	SAFROB	—
Taung						
Taung I (L)	$M_{\overline{1}}$	SAFROB/ SAFGRA	SAFROB/SAFGRA (C6/no C7)	SAFROB	SAFROB	NA

A dash indicates where the method does not discriminate between taxonomic categories for the particular tooth type.
'NA' indicates cases where damage, poor preservation, wear or lack of access has prevented the observations or measurements being made.

taxonomic categories are discrete enough to suggest that it may be possible to use the combination of information about absolute size and crown shape as a guide to the taxonomic affinities of problematic specimens.

The taxonomic implications of the results of the two studies for specimens in the 'unknown' category are summarized in Table 8. The taxonomic allocations in the crown area column indicate whether the measured crown base area of a specimen is within 2 S.D.s of the mean of a taxonomic category and the allocations under the heading of additional cusps are based on the information given in Table 11 of Wood & Abbott (1983). The allocations on the basis of relative cusp area and fissure pattern indicate which group centroid is closer to the 'unknown' specimen in the two analyses; when the distances to the centroids differ insignificantly, the nearest centroid is listed first. The assignments in the crown profile column refer to a simple visual assessment of the cross section, and depend on the homogeneity of the patterns, and the size of the sample within each taxonomic group.

Of the specimens from East African sites, the results of analysing the shape of the molar in the mandible KNM–ER 1820 and the isolated molar, OH 30, confirm the conclusions, based on their absolute size, that they most closely resemble the shape of the lower molars in the EAFROB taxonomic category. The mandibles, KNM–ER 1506 and 1802 are of interest because, including as they do both the first and second molars, they provide two opportunities to assess the affinities of these specimens. In both cases, the balance of the information about the shape of the molar crowns suggests that these teeth more closely resemble those in the EAFHOM group than they do molars belonging to the EAFROB category (Table 8), though the $M_{\overline{1}}$ of KNM–ER 1506 shows a mix of features. In the case of KNM–ER 1802, while the $M_{\overline{1}}$s are clearly closer to the EAFHOM centroid, the $M_{\overline{2}}$ distances suggest that these teeth show similarities to all taxonomic categories except EAFROB.

In terms of absolute size, both SK 1587 (three molar crowns in a damaged mandible) and SK 1588 (a single molar crown in a left mandibular fragment) fall in the overlap zone between the SAFROB and SAFGRA taxonomic categories. When crown shape is examined, however, the presence of a C6 in all three molars of SK 1587, the relative size of the cusps, the disposition of the fissures and, in the case of the $M_{\overline{1}}$, the crown profile, all point to this specimen having affinities with the SAFROB category. The affinities of SK 1588 are also with the SAFROB group, but the evidence is less strong.

The last 'unknown' specimen to be considered is the left $M_{\overline{1}}$ from Taung. Its absolute size and complement of additional cusps make its taxonomic position equivocal, but, in terms of relative cusp size and fissure pattern, it is closer to the pattern found in the SAFROB group than it is to the SAFGRA category. Tobias (1973, 1981) has, in the past, questioned the taxonomic affinities of Taung, but clearly the form of the first mandibular molar is only one of a series of morphological features which will have to be examined before the affinities of this historically and taxonomically important specimen can be satisfactorily reviewed.

CONCLUSIONS

Although dietary differences between early hominid taxa have been emphasized by some authors (e.g. Robinson, 1962; Grine, 1981), recent research on jaw biomechanics and enamel microwear (Walker, 1978, 1981) has shown that previous assumptions about the nature of the 'robust' australopithecine diet may have been mistaken. Walker's conclusion, albeit tentative, is that the 'robust' australopithecines may have persisted with a form of the original hominoid diet, which was probably based on the ingestion and mastication of whole fruits. This assessment of evidence from diverse sources, coupled with the results of analyses of mastication which suggest that all hominids, and indeed members of the Hominoidea (Mills, 1955, 1963, 1978; Walker, 1981) share a basically similar masticatory pattern, makes it unlikely, therefore, that any marked differences would be found between the molar teeth of early hominid taxa. Indeed, a recent review of the fossil evidence has suggested that intertaxonomic differences in mandibular molar form are relatively subtle (e.g. Howell, 1978), and the features cited in diagnoses of these taxa usually relate to either the overall size of molar teeth or their size relative to that of the incisors and canines.

The results of this analysis of the shape of early hominid mandibular molar crowns confirms this relative uniformity of structure, and the Pythagorean distances given in Table 7 show that, with the exception of the distances between the EAFROB centroid and those of EAFHOM and SAFGRA the distances between group centroids are of the same order as the average distance between specimens within each of the major taxonomic categories.

Thus, while the results relating to the affinities of some of the 'unknown' specimens are of interest, the main purpose of this investigation has been to explore the ways in which dental morphology can be exploited for the systematic assessment of early hominid remains. Erdbrink (1965, 1967), Corruccini (1977*a*, *b*, 1978*a*) and Lavelle (1978*a*, *b*) were the first to explore the potential of a detailed suite of measurements for analysing primate dental material. Lavelle (1978*a*) concluded (we believe correctly) that "objective examination and investigation of teeth will only be achieved by a metrical approach", and went on to propose that, in order to obtain an accurate metrical definition of a tooth, many dimensions are required, and that such multidimensional data call for multivariate statistical methods for their analysis.

We have, however, taken care in this study to analyse the data by simple methods before proceeding to use complex multivariate techniques. The advantage of the latter methods is that they not only allow the assimilation and manipulation of a range of variables simultaneously and with due regard to the correlations between them, but they also provide a means of visualizing the relationships between specimens. However, the other, and equally important, emphasis of this pilot study has been to develop objective ways of describing tooth crowns metrically, and to this end we have concentrated on investigating their shape as well as their size.

There is little doubt that the methods we have used in this study can be improved and refined, but, nonetheless, we believe that they provide the basis of a system which can be used to examine the postcanine dentition of fossil and extant higher primates. Such techniques will be particularly useful in the analysis of fossil collections which contain large numbers of often unassociated isolated teeth, e.g. the Omo (Coppens, 1981).

The next paper in this series will explore the pattern of differences in the form of the mandibular premolar crown, and preliminary results suggest that these teeth show more variation between hominid taxa than do mandibular molars. It is also our intention to extend the range of fossils to include the Miocene hominoids, and thus enable us to attempt to trace the evolutionary development of the substantial differences that exist between the postcanine teeth of *Homo sapiens* and those of the extant apes.

SUMMARY

Accurate measurements of the absolute and relative size of individual cusps, the arrangement of the primary fissure system and the shape of coronal cross sections of the tooth crown have been used to investigate the pattern of variation in Plio-Pleistocene hominid mandibular molar teeth. Teeth were either grouped into one of six taxonomic categories or considered as individual cases.

Univariate analysis of relative cusp areas shows that the two taxonomic categories of 'robust' hominids from East and Southern Africa have relatively small mesial cusps, but a relatively large entoconid and hypoconulid and Principal Component plots of the data show that the 'robust' categories can be distinguished on the basis of relative cusp size. Other evidence suggests that these differences are not likely to be the result of allometric phenomena. Fissure pattern was analysed using the X/Y coordinates of defined reference points. Patterns were compared by Procrustes analysis and the relationships between teeth contained in the resulting similarity matrix were portrayed using Principal Coordinates plots and a nearest neighbours table. The positions of the posterior fovea and the mesial longitudinal fissure were important for distinguishing taxonomic categories. The shape of the coronal profiles proved difficult to quantify, but there were consistent and distinct differences between the South African 'robust' sample and teeth included within the East African *Homo* category.

When these results are combined with those of a previous study of overall crown size and the distribution of extra cusps, they allow the affinities of isolated teeth or contentious specimens to be assessed. For example, our results show that KNM–ER 1506 and 1802 are more similar to the East African *Homo* group than any other category, and they indicate that though SK 1587 and 1588 are small teeth, they nonetheless are closest to the South African 'robust' category in terms of relative cusp size, fissure pattern and crown profile shape. The closest affinities of the Taung First mandibular molars are also with the South African 'robust' sample.

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